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STUDY ON THE PHYLOGENY OF PEMPHIGIDAE (HOMOPTERA: APHIDINEA)

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Abstract The phylogeny of Pemphigidae (Homoptera: Aphidinea) is studied using cladistic method. The monophyly of traditional Schlechtendalini, Fordini and Pemphigini are recognized, while traditional Prociphilini and Tetraneurini are found to be paraphyletic groups. Moreover, Fordinae and Pemphiginae have closer phylogenetic relationship with each other than with others. *Formosaphis* is transferred from Pemphiginae to Fordinae accordingly.

Key words Pemphigidae aphids, cladistic analysis, phylogeny

1 INTRODUCTION

Most species of Pemphigidae aphids are dioecious, producing galls or leaf curling on the primary hosts. Some species migrate to roots of woody secondary hosts, others to roots or aerial parts of herbaceous secondary hosts. The Pemphigidae consists of three subfamilies: Eriosomatinae, Pemphiginae and Fordinae[1]. Up to now, the phylogeny of Pemphigidae has not been studied using cladistic method. The phylogenetic relationship of three subfamilies is obscure[1~4]. The phylogenetic relationships among genera of each subfamily are not clear too. In order to understand the phylogeny of Pemphigidae better, this study was carried out.

Some Pemphigidae aphids only make leaves curling, others produce opened-galls or pseudo-galls on leaves, and some aphids produce closed-galls on twigs, petioles or leaf veins. These harming behaviors show two evolution traits: (1) make leaf curling→produce pseudo-galls→produce primary opening galls→produce secondary opening galls and (2) damage on leaves→damage on leaf veins→damage on main leaf veins, petioles or twigs. In this paper, not only morphological characters, but also above ecological characters are chosen for the cladistic analysis. We believe that ecological characters are very important for the re-construction of Pemphigidae's evolutionary history.

2 MATERIALS AND METHODS

28 genera of Pemphigidae, representing most genera of Pemphigidae, are taken as in-group members. The list of their names is shown in Table 1.

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Because the sister group of Pemphigidae is unknown, five families, Adelgidae, Phylloxeridae, Mindaridae, Phloeomyzidae and Hormaphididae were chosen as a composite out-group. As Adelgidae owns many primitive characters, it is considered as the chief out-group. Other out-groups are considered only when the polarity cannot be decided according to Adelgidae ' s characters. Character polarities are established through standard out-group analysis[5].

21 morphological and 4 ecological characters are considered (shown in Table 2).

Calculation of phylogenetic relationships was accomplished with the aid of the computer program HENNIG86 version 1.5 (Farris, 1988). The primitive data matrix is shown in Table 3.

3 CLADISTIC ANALYSES

Analysis 1 Exhaustive search was carried out by using "ie" option. After 8 hours operating, the result did not emerge. "mh * " and "bb * " options had to be used in the next search. This time the result emerged as "length = 100, ci = 40, ri = 69, trees = 3159 (overflow). Because it was not known whether the shortest tree was among above 3159 trees, the successive weighing procedure could not be used in the next step.

3159 trees were skimmed through. Among the majority of trees, Pemphiginae and Fordinae were monophyletic groups. However, the monophyly or paraphyly of Eriosomatinae was uncertain.

Table 1 The list of ingroup members
表 1 内群成员

In-group members
Aphidounguis Takahashi, 1963
Aploneura Passerini, 1863
Baizongia Rondani, 1848
Chaetogeoica Remaudière & Tao, 1957
Colopha Monell, 1877
Colophina Börner, 1932
Dimelaphis Zhang, gen. nov. ined.
Epipemphigus Hille Ris Lambers, 1966
Eriosoma Leach, 1818
Floraphis Tsai & Tang, 1946
Forda von Heyden, 1837
Formosaphis Takahashi, 1925
Geoica Hart, 1894
Kaburagia Takagi, 1937
Kaltenbachiella Schouteden, 1906
Meitanaphis Tsai & Tang, 1946
Mimeuria Börner, 1952
Namaforda Zhang, 1998
Nurudea Matsumura, 1917
Pachypappa Koch, 1856
Pachypappella Baker, 1920
Paracletus von Heyden, 1837
Pemphigus Hartig, 1839
Prociphilus Koch, 1857
Schlechtendalia Lichtenstein, 1883
Smynthurodes Westwood, 1849
Tetraneura Hartig, 1841
Thecabius Koch, 1957

Analysis 2 In general, three subfamilies of Pemphigidae separately use Ulmaceae, Salicaceae and Anacardiaceae as their primary host plants. This conclusion has been accepted by the majority of aphidologists. The primary host plants have overwhelming importance in aphid ' s study. So the monophyly of Pemphigidae subfamilies can be accepted without too much dubiousness. However, the paraphyly of Eriosomatinae might be remained.

Table 2 List of characters and character states used in the phylogenetic analysis

（“0”represents the plesimorphic state，“1”，“2”，“3”，“4”represent derived character states，the general character polarities，except for characters 4 and 24，are consistent with the direction of 0→1→2→3→4）

表2 支序分析所选用的特征及特征状态

（“0”代表祖征，“1”，“2”，“3”，“4”代表离征，极性除特征4和24外趋向为0→1→2→3→4）

1. The head of alate adults without epicranial suture（0）；The head of alate adults with epicranial suture（1）
2. Alate adults with the length of antennal segment Ⅲ shorter than or as long as the length of antennal segments Ⅳ＋Ⅴ＋Ⅵ（0）；Alate adults with the length of antennal segment Ⅲ obviously longer than the length of antennal segment Ⅳ＋Ⅴ＋Ⅵ（1）
3. Alate adults without a big-plate-shaped secondary rhinaria on antennae segments Ⅲ～Ⅵ（or Ⅴ）（0）；Alate adults with a big-plate-shaped secondary rhinaria on antennal segments Ⅲ～Ⅵ（or Ⅴ）（1）
4. Secondary rhinaria transverse-oval-shaped（0）；Vertical-oval-shaped（1）；Narrow-ringlike-shaped（2）；Plate-shaped（3）；Round-shaped and vertical-oval-shaped（4）

$$\begin{tikzcd}[row sep=small, column sep=small]
0 \arrow[r] & 1 \arrow[r] \arrow[d] & 2 \arrow[r] & 3 \\
 & 4 & &
\end{tikzcd}$$

5. Primary rhinaria not surrounded by distinct rings of short hairs（0）；Primary rhinaria surrounded by distinct rings of short hairs（1）
6. Secondary rhinaria not surrounded by distinct rings of short hairs（0）；Secondary rhinaria surrounded by distinct rings of short hairs（1）
7. Primary rhinaria without thick，sclerotized rims（0）；Primary rhinaria with thick，sclerotized rims（1）
8. Fore wing with bases of cubical branches united（0）；Fore wing with bases of cubical branches approached（1）；Fore wing with bases of cubical branches obviously separated（2）
9. Media of fore wing unbranched（0）；Media of fore wing branched，with one fork（1）
10. The pterostigma of fore wing normal，not extended to the apex of wing（0）；The pterostigma of fore wing strengthen，but not extended to the apex of wing（1）；The pterostigma of fore wing sickle-shaped，extended to the apex of wing（2）
11. Hind wing with two oblique veins，which separate at bases，or with only one oblique vein（0）；Hind wing with two oblique veins closes to each other at bases（1）
12. Hairs on body not spatulate（0）；Spatulate（1）
13. At least legs of apterous adults with two tarsal segment（0）；At least fore and middle legs of apterous adults with one tarsal segment（1）
14. Alate adults without siphuncular or siphuncular present in abdominal segment V（0）；Alate adults with siphuncular present in abdominal segment VI（1）
15. Alate without siphuncular（0）；With pore-shaped siphuncular（1）
16. Cauda broad-shaped（the basal width 2 times longer than its height）（0）；Cauda rounded-shaped（the basal width 2 times shorter than its height）（1）
17. Abdomen without rudimentary gonapophyses，or abdomen with one or two rudimentary gonapophyses（0）；Abdomen with three rudimentary gonapophyses（1）
18. Apterae with wax plates well developed，occurring in head，thorax and abdomen（0）；Not well developed，occurring only in part of body（1）；Not developed，not occurring in any part of body（2）
19. Wax plates generally composed by same-sized wax cells（0）；Wax plates composed by obviously different-sized wax cells and same-sized wax cells（1）
20. Wax plates developed in all morphs（0）；Wax plates developed in some morphs（1）；Wax plates developed in no morphs（2）
21. Sexupara occurring in autumn（0）；Sexupara occurring in spring（1）
22. Producing leaf-curing on the primary hosts（0）；Producing pseudo-galls or leaf nests（1）；Producing primary-opening-galls（2）；producing secondary-opening-galls（3）
23. On the primary hosts，aphids damaged on leaves（0）；On leaf veins（1）；On petioles and branches（2）
24. The primary host being primitive angiosperm plants（0）；Salicaceae（1）；Ulmaceae（2）；*Rhus*，Anacardiaceae（3）；*Pistacia*，Anacardiaceae（4）；Oleaceae，or Caprifoliaceae，or Aceraceae，or Rosaceae（5）

$$\begin{tikzcd}[row sep=small, column sep=small]
 & 5 & \\
1 & 0 \arrow[l] \arrow[r] \arrow[u] \arrow[dl] \arrow[dr] & 2 \\
3 & & 4
\end{tikzcd}$$

25. First tarsal segm. with 2，2，2 or 3，3，2 or 3，2，2 or 3，3，3 hairs in alate viviperous female（0）；First tarsal segm. with 4，4，4 or 5，3，3 or 5，5，5 or 7，7，7 or 9，9，9 hairs in alate viviperous female（1）

Table 3　Data of primitive matrix

表 3　瘿绵蚜科属间支序分析原始矩阵

Taxa	Characters				
	00000 12345	00001 67890	11111 12345	11112 67890	22222 12345
Outgroup	00000	00200	00000	00000	03000
Aploneura	10001	10000	00000	00001	1304?
Baizongia	10021	10100	00000	00000	13141
Chaetogeoica	10041	10000	00000	00000	13141
Dimelaphis	10021	10202	00?00	0?00?	1???1
Floraphis	00021	10201	00?00	10?0?	13130
Kaburagia	00130	00200	00?00	?0101	13130
Meitanaphis	00131	00202	00?00	00?0?	13130
Nurudea	00021	10100	00?00	10?0?	13130
Schlechtendalia	00??1	00102	00?00	10?0?	13130
Forda	1?040	00100	00000	00202	13041
Formosaphis	10131	00000	10000	10100	????0
Geoica	10041	00100	01000	00201	13140
Namaforda	10040	00100	00?00	00?0?	1304?
Paracletus	10040	00100	00000	002?2	1004?
Smynthurodes	10040	01200	00000	002?2	1304?
Epipemphigus	00011	10200	1000?	00101	01011
Mimeuria	?0021	00100	10101	00000	0005?
Pachypappella	?0041	00110	10000	01100	02010
Pachypappa	00011	?0210	10000	00101	02010
Pemphigus	00021	00200	1000?	01100	02211
Prociphilus	10021	00200	10000	01000	00050
Thecabius	?0011	00200	10000	01100	01011
Aphidounguis	00021	00200	00011	000?1	01020
Colopha	10021	00210	0010?	00011	02120
Colophina	1?020	00010	00001	00011	0???0
Eriosoma	01021	00210	00001	00011	01020
Kaltenbachiella	10021	00200	00000	10011	03120
Tetraneura	00021	00100	0010?	00011	03020

In order to analyze the phylogenetic relationship among three subfamilies，a new matrix（subfamily matrix）was built up by using characters 17，21，11，19，20，4，13，9，new character 1，new character 2 and character 25. New character 1 is that "apterous adults on the second host plant without siphuncular（0）or with siphuncular（1）". New character 2 is that "antenna of alate female with 5- or 6-segments（0）or with only 6-segments（1）". Each character state was defined by the majority state of subfamilies. The subfamily matrix is shown in Table 4.

Table 4　Data of subfamily matrix

表 4　瘿绵蚜科亚科间支序分析原始矩阵

Taxa	Characters		
	12112 71190	20010 04439	222 675
outgroup	00000	00000	000
Eriosomatinae	00010	10111	110
Pemphiginae	10100	10000	001
Fordinae	01001	11000	001

Analysis 3　In order to understand the phylogenetic relationship among genera of Fordinae，the matrix of the section from the out-group to *Smynthurodes* in Table 3 was regarded as the primitive matrix of Fordinae.

Analysis 4　In order to analyze the phylogenetic relationship among genera of Pemphiginae，the matrix of the section from *Epipemphigus* to *Thecabius* in Table 3 was regarded as the main part of the Pemphiginae primitive matrix. And the out-group line in Table 3 was added to the Pemphiginae primitive matrix as the first line. In addition，because *Formosaphis* has argued position either in Fordinae or in Pemphiginae，*Formosaphis* line in Table 3 was added to the Pemphiginae primitive matrix as the final line.

Analysis 5　In order to analyze the phylogenetic relationship among genera of Eriosomatinae， the matrix of the section from *Aphidounguis* to *Tetraneura* in Table 3 was regarded as the main part of Eriosomatinae primitive matrix . And the out-group line in Table 3 was added to the Eriosomatinae primitive matrix as the first line.

Analysis 6 In order to resolve the argued position of *Formosaphis*, the matrix of the section from the out-group to *Thecabius* in Table 3 was regarded as the matrix of Fordinae + Pemphiginae.

The subfamily matrix, the Fordinae matrix, the Pemphiginae matrix and the Eriosomatinae matrix were separately operated by using ie * options. However, the Fordinae + Pemphiginae matrix was operated by using mh * option (ie * option could not give out result and mh * + bb * option made trees overflowing).

4 RESULTS AND DISCUSSION

Results 1 (for Analysis 3) By using "ie" option, the result for Fordinae matrix is "l = 52, ci = 55, ri = 68, trees = 267." Then by using "w" option and after 2 runs, the result becomes stable. It is "l = 215, ci = 80, ri = 88, trees = 138." Fig.1 is the strict consensus tree of these 138 trees.

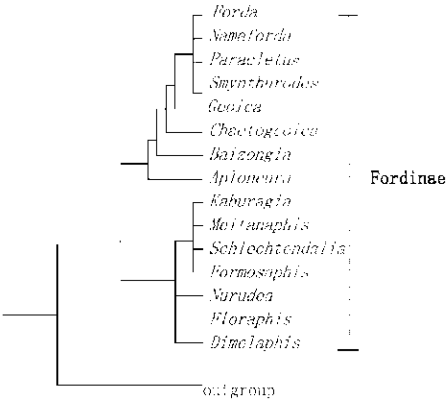

Fig. 1 The strict consensus
tree of Fordinae matrix
图1 Fordinae矩阵的系统发育关系合意树

In Fig.1, the traditional Schlechtendalini and Fordini[1] are monophyletic groups. In Schlechtendalini, *Kaburagia*, *Meitanaphis*, *Schlechtendalia* and *Formosaphis* have closer phylogenetic relationship with each other than with *Dimelaphis*, *Florophis* and *Nurudea*. In Fordini, *Forda*, *Namaforda*, *Paracletus* and *Smynthurodes* have closer phylogenetic relationship than with *Aploneura*, *Baizongia*, *Chaetegeo* and *Geoica*.

In Schlechtendalini, the phylogenetic relationships among *Kaburagia*, *Meitanaphis*, *Schlechtendalia* and *Formosaphis* are unstable. In Fordini, the phylogenetic relationships among *Forda*, *Namaforda*, *Paracletus* and *Smynthurod* are unstable too. These instabilities might be the just reason why 138 trees were gained by using "ie" option.

Results 2 (for Analysis 4) By using "ie" option, the result for Pemphiginae matrix is "l = 35, ci = 76, ri = 63, trees = 5." Then by using "w" option and after 2 runs, the result becomes stable. It is "l = 209, ci = 93, ri = 88, trees = 1 (Fig.2)"

In Fig.2, the traditional Prociphilini[1] is paraphyletic and traditional Pemphigini[1] is monophyletic.

Characters used to divide traditional Prociphilini and Pemphigini are "the length of empodinal hairs length in newborn virginogeniae", "types of secondary hosts" and "presence or absence of pale subapical zone of apical segment of rostrum". These characters are not used in this paper for their unstability sometimes.

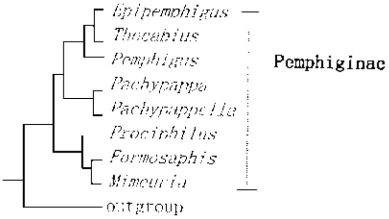

Fig. 2　The strict consensus tree of Pemphiginae matrix
图 2　Pemphiginae 矩阵的系统发育关系合意树

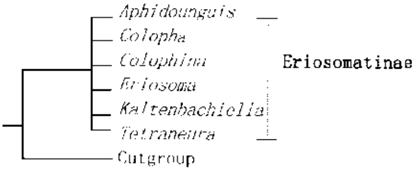

Fig. 3　The strict consensus tree of Eriosomatinae matrix
图 3　Eriosomatinae 矩阵的系统发育关系合意树

In Fig.2, two definitely monophyletic groups are *Proc-Mime* group and *Pach-Thec* group. The common-shared derived characters for *Proc-Mime* group are their primary host plant. The common-shared derived characters for *Pach-Thec* group are their primary host plant and wax plates occurring on part of body. These common-shared derived characters usually are stable and reliable. To re-divide tribes of Pemphiginae by these characters is suggested.

Results 3 (for Analysis 5)　By using "ie" option, the result for Eriosomatinae matrix is "l=24, ci=75, ri=50, trees=14." Then by using "w" option and after 1 run, the result becomes stable. It is "l=200, ci=80, ri=60, trees=14." Fig.3 is the strict consensus tree of these 14 trees.

In Fig.3, the traditional Tetraneurini[1] is paraphyly and the traditional Eriosomatini[1] might be monophyly or paraphyly. Because the members of Tetraneurini have no obvious common-shared derived characters, the paraphyly of Tetraneurini did not surprise us. For example, "segment 3 as long as or shorter than segment 4+5+6" is an important character to divide traditional tribes. However, it is an ancestoral character. Other ones used in dividing Tetraneurini and Eriosomanae also overlap with each other. In addition, only one genus of Eriosomatini was included in our analysis, so the monophyly or paraphyly of Eriosomatini still can not be determined here.

Among 6 genera of Eriosomanae, there is no dominant closer phylogenetic relationship between any two of them. Therefore to re-appraise characters or add some new characters for the future phylogenetic study of Eriosomanae is needed.

Results 4 (for Analysis 6)　In order to decide the argued position of *Formosaphis*, "mh*" option was used for the Pemphiginae+Fordinae matrix. The result is "l=79, ci=45, ri=70, trees=6." Fig.4 is the strict consensus tree of these 6 trees.

Traditionally, *Formosaphis* belongs to Pemphiginae[2,4]. However, *Formosaphis* belongs to Fordinae in Fig.4 *Formosaphis* has a big plate-shaped secondary rhinaria, which is very like the shape of some species of Fordinae. The taxonomic position of *Formosaphis* has been doubted before this work. Through above careful analysis, to put *Formosaphis* in Fordinae seems more reasonable.

Results 5 (for Analysis 2)　By using "ie" option, the result for the subfamily matrix is "l=

13, ci=100, ri=100, trees=1." Fig.5 is the tree.

In Fig.5, Pemphiginae and Fordinae have closer phylogenetic relationship with each other than with Eriosomatinae, and Eriosomatinae closer to out-group than Pemphiginae and Fordinae.

The common-shared derived character of Pemphiginae and Fordinae is that "alate viviparous female with 5, 5, 5 or 4, 4, 4 or 7, 7, 7 hairs in first tarsal segment".

In addition, because *Formosaphis* has both characters of Pemphinae’s wing and characters of Fordinae’s secondary rhinaria, closer phylogenetic relationship between Pemphiginae and Fordinae than between other two subfamilies is implied. On the other hand, in Takhtajan’s classification of plants[6], Salicaceae and Anacardiaceae have closer phylogenetic relationship than with Ulmaceae. So, the phylogenetic relationship reflected from host plants is also consistent with the phylogenetic relationship reflected from aphids (Fig.5).

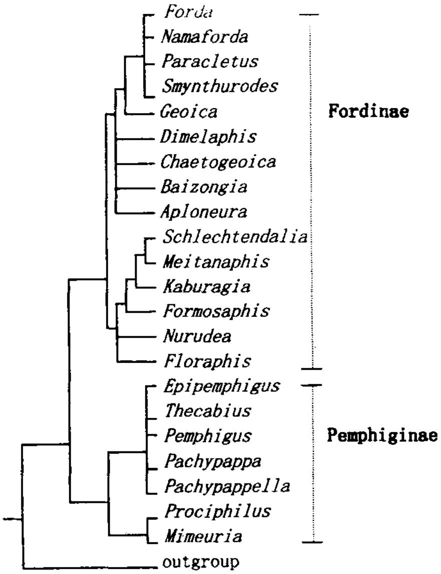

Fig. 4 The strict consensus tree of Fordinae + Pemphiginae matrix

图 4 Fordinae + Pemphiginae 矩阵的系统发育关系合意树

Results 6 In Fig.5, by using Fig.1 in place of Fordinae, using Fig.3 in place of Eriosomatinae, using Fig.2 in place of Pemphiginae and remove *Formosaphis* off, a new figure (Fig.6) is gained.

According to our present data and understanding, Fig.6 might best reflect the phylogeny of Pemphigidae.

Results 7 Because *Formosaphis* and *Dimelaphis* belong to Schlechtendalini, and the primary host plants of Schlechtendalini usually belong to plants of *Rhus*, the primary host plants of *Formosaphis* and *Dimelaphis*, whose primary hosts have not been known till now, are predicted being some species of *Rhus*.

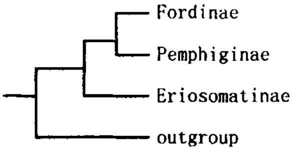

Fig. 5 The tree of subfamily matrix

图 5 瘿绵蚜科亚科间系统发育关系支序图

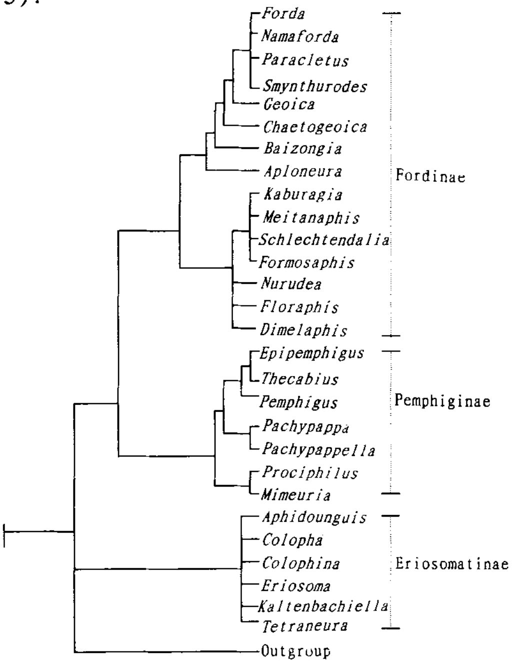

Fig. 6 The suggestion of the phylogenetic relationship among genera and subfamilies of Pemphigidae

图 6 瘿绵蚜科属间及亚科间系统发育关系

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我国及邻近地区斑腿蝗科区系及其起源研究*

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摘要　根据斑腿蝗科（Catantopidae）在我国各动物地理区的种类组成和区系特点，发现华中区和华北区的区系特点不明显，前者为南北成份的混交区，后者特有种可跨区分布，这与蝗虫有明显的区域和地带分布的特点不相符。为此，作者同意马世骏先生把江汉平原、秦阳山山地、辽黄淮平原划为古北区，成为东方区系。根据我国北方种类与前苏联西伯利亚区系关系密切，而极少数种类与前苏联欧洲部分甚至欧洲部分所共有这种事实，认为世界动物地理区划中应把西伯利亚单独作为一个亚区较合适。

关键词　区系，起源，斑腿蝗科

1　我国斑腿蝗科的区系特点

1.1　种类丰富

我国幅员辽阔，自然条件复杂，按自然条件的不同可分为东部季风区和西部干旱区，两种不同的自然条件繁衍着丰富的动物种类，斑腿蝗科（Catantopidae）这个类群也不例外。

斑腿蝗科全世界已知有 3 000 多种，我国有详细分布记录的有 92 属 319 种，约占世界总数的 1/10。

1.2　各地理区种类丰富度不一

我国斑腿蝗科种类很丰富，但它们在我国各动物地理区的占有数却差异很大。我国华中、西南、华南区的种类远比东北、华北等地区丰富[1]。

1.3　地理成分较单一

地理成分是根据分布类型而定的，它能反映区系成分和地理渊源，我国斑腿蝗科种的地理成分较单一，体现在：

（1）与世界其它动物地理区共有种少。我国斑腿蝗科有 19 属与世界其它洲共有[1]，但与非洲、澳洲及北美洲的共有种数仅分别为 2，1，2 种。

（2）广布种少。已知 319 种中仅 8 种为广布种，占 2.5%，其余或者为东洋种或者为古北种。

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